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珊瑚共生体对 UV 辐射与 CO_2 浓度变化的生理学响应

Physiological Responses of Coral Symbiont to Changes of UV radiation and CO_2 concentrations

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摘要

大气 CO_2 浓度升高导致了全球变暖与海洋酸化，并引起海水中有色可溶性有机物减少，使得海水透明度增加，提高了进入水体的紫外辐射（UVR，280－400 nm）水平，从而对浅水珊瑚礁生态系统的各种生物过程造成影响。另一方面，海洋酸化及环境中 pH/CO_2 的扰动，也会影响珊瑚及其与藻类的共生关系。本博士论文，以鹿角杯形珊瑚（*Pocillopora damicornis*）为研究对象，探讨了 UV 辐射对其共生藻日释放量的影响；同时，研究了鹿角杯形珊瑚和浅杯排孔珊瑚（*Seriatopora caliendrum*）浮浪幼体对阳光 UV 辐射变化的响应。在此基础上，揭示了 UV 辐射对浮浪幼体及其共生藻的影响。另外，还研究了一种系群 D 共生藻（CCMP2556）对海水中 pCO_2 昼降夜升的生理学响应，并探讨了 pCO_2 升高与 UVR 对其的复合效应。主要的结果如下：

1. 阳光辐射变化影响鹿角杯形珊瑚释放共生藻的量。UV 辐射显著降低了鹿角杯形珊瑚色素（包括叶绿素 *a* 和类胡萝卜素）和紫外吸收物质（UVACs）的含量，导致珊瑚共生藻的日平均释放速率提高了 10－20%（95%置信区间上不显著）。有 UV 和无 UV 辐射处理间的日变化模式相似，即正午时共生藻的释放达到最高峰，但 UV-B（280－315 nm）的存在使得这一高峰期提前了 1 小时。
2. 不同种类的珊瑚幼体对 UV 辐射的响应不同。与分布较深的浅杯排孔珊瑚相比，分布较浅的鹿角杯形珊瑚的浮浪幼体，对 UV 辐射的敏感性高，幼体内共生藻光合作用受抑制的程度也较大。在 UV 辐射的作用下，鹿角杯形珊瑚幼体共生藻的净光合速率下降了 75－85%，其叶绿素 *a* 和 UVAC 含量与温度变化的相关性大。UV-A（315－400 nm）显著抑制了鹿角杯形珊瑚幼体的发育，其对幼体的成活率、变态率与附着率的抑制率达 22－25%。浅杯排孔珊瑚幼体内的共生藻平均密度，受 UV 辐射的影响，反而升高。UV-A 辐射促进了共生藻的有效光化学效率，而 UV-B 可抵消 UV-A 的促进作用；UV-A 降低了该珊瑚幼体的变态速率。
3. 海水 pCO_2 升高和昼降夜升（460－1000 μatm）都使得共生藻对无机碳的浓缩能力（CCMs）发生了上调，但二者间有着不同的上调模式。pCO_2 的增加促

进了共生藻细胞的比生长速率，降低了细胞内叶绿素 *a* 和类胡萝卜素的含量。同时，共生藻 PSII 的有效光化学截面积减小了，且 Q_A 的周转时间延长了，表观光能利用效率降低了；然而，其单位叶绿素 *a* 的光合放氧速率和呼吸速率分别提高了 49%和 41%；单位细胞的光合与呼吸速率均未受到影响。此外，pCO_2 的增加使得 K_m(DIC)的值降低了 63%，而 $K_m(CO_2)$稳定在 3.0－3.4 μmol L^{-1}，提高了细胞对 HCO_3^-的亲和力。pCO_2 的昼降夜升降低了细胞内类胡萝卜素的含量。与 pCO_2 的增加类似，pCO_2 的昼降夜升使得 PSII 的有效光化学截面积减小，并延长了 Q_A 的周转时间，但 PSII 的有效光化学效率提高了 27%，非光化学淬灭下降了 34%，虽然如此，其光合放氧速率并未提高，且呼吸速率要明显低于高 CO_2 处理（19%）。此外，pCO_2 的昼降夜升使得胞内碳库增大了近一倍。

4. pCO_2 升高与 UV 辐射对共生藻有拮抗作用。在 UV 辐射处理下，共生藻细胞的捕光色素含量下降，而 pCO_2 的增加使得其含量明显增加。同时，UV 辐射促使共生藻细胞 K_m(DIC)增加了 43－62%，$K_m(CO_2)$也相应提高了 43－64%，降低了细胞对无机碳的亲和力，而 pCO_2 的增加造成细胞 K_m(DIC) 和 $K_m(CO_2)$都下降了 27－50%，即 CCMs 显著上调。同时，细胞的呼吸速率在二者的拮抗作用下，分别下降了 22－39%（LC：低 CO_2 处理）与增加了 33－36%（HC：高 CO_2 处理）。此外，在 UV 辐射下，HC 细胞对 UV-A 损伤的修复速率要明显高于 LC 细胞，但在培养光强下，LC 细胞对 UV-A 损伤的恢复速率要比 HC 细胞快了 33%。UV-A 对细胞的表观光能效率、最大电子传递速率和光饱和参数具有抑制作用，而 UV-B 的存在抵消了这一作用，pCO_2 的增加使得细胞对 UV 的敏感性降低，缓解了紫外辐射的效应。

总之，UV 辐射，虽然对珊瑚共生藻的释放没有显著影响，但会抑制幼体的变态与附着过程，并抑制共生藻的光合作用。pCO_2 的增加与昼降夜升都会提高共生藻对无机碳的利用能力，但在昼降夜升下光合或生长速率并未增加，说明 CO_2 的扰动导致共生藻能耗增加。UV 辐射和 pCO_2 升高产生了拮抗效应，高 CO_2 下，细胞对 UV 的敏感性下降。然而，原位复杂环境下，分布不同海域、不同深度的珊瑚及共生藻，经受阳光 UV 辐射的程度不同，对 CO_2 升高的响应，会存在较大的区域性差别。

关键词：珊瑚幼体；共生藻；紫外辐射；海洋酸化

Abstract

Rising atmospheric carbon dioxide (CO_2) is causing ocean acidification and ocean warming, with reduced amount of colored dissolved organic matter in the water. Ultimately, the coral reef water may become clearer and the transmission of ultraviolet radiation (UVR, 280-400 nm) into the oceans would be enhanced, which would affect various biological processes in shallow coral reef ecosystem. On the other hand, ocean acidification and the fluctuation in pH/pCO_2 may also influence the symbiosis between coral and the dinoflagellate *Symbiodinium*. In this study, the release rate of *Symbiodinium* from the coral *Pocillopora damicornis* was studied under UVR stress. Moreover, the responses of the planula larvae of *P. damicornis*, as well as that of *Seriatopora caliendrum*, to UV radiation were investigated, and the effects of UVR on the symbiotic algae within the larvae were examined. In addition, by adjusting pCO_2 fluctuating regimes (constant versus oscillatory), the effects of high pCO_2 and diel variation in pCO_2 on the physiological performance of *Symbiodinium* CCMP2556 were studied, and the combined effects of elevated CO_2 and UVR were also examined. The main results are as follows:

1. Solar radiation modulated the diurnal release pattern of *Symbiodinium* from the coral *P. damicornis*. The UVR exposure significantly reduced the content of chl *a* and carotenoids per surface area in the coral branch, as well as that of the UV-absorbing compound (UVAC) at the end of experiment. The release rate was higher in the exposure to UVR by ~10-20%, but this increment was not significant at the 95% confidence level. The diurnal release pattern of *Symbiodinium* with or without UVR were similar, i.e. the release rate peaked at noon (11:00-13:00), while the time was advanced for an hour when exposed to UV-A (315-400 nm) and UV-B (280-315 nm).

2. The larvae of two coral species responded differently to UVR stress, with larvae of *P. damicornis* from shallower water being more sensitive to UVR exposure than *S. caliendrum* from deeper water, so as the inhibition to the photosynthesis of *Symbiodinium* in the larvae. UVR stress decreased net photosynthetic rate of endosymbiotic alga in *P. damicornis* larvae by 75-85%. There was a positive relationship between significance of differences in chl *a* and temperature, which

also occurred between the concentration of UV absorbing compounds and temperature. The development of *P. damicornis* larvae was severely inhibited by UV-A, with the inhibition rate of survivorship, metamorphosis and settlement ranging around 22-25%. The density of *Symbiodinium* in *S. caliendrum* larvae exposed to UVR was obviously higher than the control. The effective photochemical efficiency (Fv'/Fm') of *Symbiodinium* in *S. caliendrum* larvae was stimulated by UV-A, but the stimulation was offset by UV-B. UV-A obviously delayed the metamorphosis and settlement of *S. caliendrum* larvae.

3. Increased pCO_2 and day-night fluctuation of pCO_2 up-regulated the carbon concentrating mechanisms (CCMs) of *Symbiodinium* (CCMP2556). After acclimation to high pCO_2 environment for over 15 generations, the *Symbiodinium* showed significant higher growth rate, while the content of chl *a* and carotenoids per cell decreased. At the same time, the functional absorption cross-section of PSII ($Sigma(II)_{440}$) and the apparent photosynthetic efficiency (α) derived from light curve in 440 nm decreased, with the increase of time constant of Q_A turnover (τ). The photosynthetic oxygen evolution and respiration rates per chl *a* were enhanced by 49% and 41%, respectively, whereas both rates normalized to per cell were unchanged. In view of the carbon utilization, increasing pCO_2 significantly decreased the half-saturation concentration for DIC ($K_m(DIC)$) by 63%, while the $K_m(CO_2)$ stabilized at 3.0 to 3.4 μmol L^{-1}, and the affinity to HCO_3^- was thus enhanced. Variable pCO_2 (oscillating between 460/1000 μatm) caused the evident decrease of cellular carotenoids content, being similar with the effects of increasing pCO_2, $Sigma(II)_{440}$ decreased and τ increased, while the effective quantum yield of PSII (Fv'/Fm') increased by 27% and non-photochemical quenching (NPQ) lowered by 34%. Moreover, the respiration rate of *Symbiodinium* was lower by 19% under diurnal fluctuating pCO_2, compared to that of the algae under increasing pCO_2 treatment. In face of variation of pCO_2, *Symbiodinium* up-regulated the CCMs by nearly doubling the internal carbon pool, without altering the carbon affinity.

4. An antagonistic effect occurred when elevated CO_2 was combined with UVR. Exposure to UVR reduced the cellular contents of chl *a* and chl *c*, but the inhibition was reversed when combined with increased pCO_2. In addition, upon UVR exposure, $K_m(DIC)$ and $K_m(CO_2)$ of *Symbiodinium* increased by 43-62% and 43-